A DEVONIAN LYCOPOD STEM WITH WELL-PRESERVED CORTICAL TISSUES

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ABSTRACT. *Phytokneme rhodona* is a new genus and species of lycopod stems from the late Devonian of Kentucky, U.S.A. The description is based on an unbranched axis a little over 3 cm in diameter in which the gross cellular preservation is essentially perfect. The cylindrical core of primary xylem is surrounded by a few radially aligned tracheids. The middle cortex is unique, being composed of a ground tissue of irregularly shaped but essentially isodiametric cells and a network of ray-like strands; the outer cortex is composed of elongate fibrous cells. The leaf traces depart in a low spiral producing a nearly whorled arrangement. In the outer cortex each trace is accompanied by a large chambered air space; otherwise there is no aerenchymatous tissue in the stem. This is perhaps the best-preserved Palaeozoic lycopod stem that has been found to date and adds to our knowledge of the extra-stelar tissues.

THE following account is based on a remarkably well-preserved lycopod stem from the Devonian of Kentucky, U.S.A. It is of special interest because the cortical tissues, which are almost invariably poorly preserved or quite lacking in Palaeozoic petrified lycopod specimens, are essentially intact. The cellular structure of the entire stem is preserved with the exception of a part of the phloem; however, even this is intact in some parts of the specimen.

A few other Palaeozoic lycopod stems have been found with the cortical tissues preserved. We believe that the photographs of our Kentucky specimen testify to the outstanding excellence of its preservation and it is worth placing on record on that account alone. However, where significant comparisons are possible, they do not seem to be close enough to justify the use of any previously established binomial. There is a possibility that the fossil may be the stem of the plant that bore the cone *Lepidostrobus kentuckiensis* Scott, 1915 (see also Scott and Jeffrey 1914). Certain differences in the anatomy of the two, and the fact that they were not found in organic connection, render it inadvisable to imply a relationship that we cannot be certain of, we have therefore chosen to describe the fossil under a new name.

Several recent studies of the Palaeozoic lycopods have emphasized their distinctive cauline anatomy as well as their extraordinary if not unique growth habit and physiology. For example, studies by Arnold (1960) and Lemoigne (1966) indicate that the vascular cambium produced only secondary xylem. Investigations by Andrews and Murdy (1958) and by Eggert (1961) have been concerned with the ontogeny of certain arborescent species; apparently the trunk or primary axis attained a height of many metres in some cases before the initial division took place; this was followed by numerous dichotomies, equal or unequal, which resulted in progressively smaller branch orders, to a certain minimum point at which growth ceased. This is quite in contrast to the growth pattern of other groups of plants such as the arborescent Dicotyledoneae and Coniferae.

Our study is based on a single petrified specimen of a lycopod axis 28 mm in diameter and about 24 cm long. S. R. Ash informed us (personal communication 1969) that the

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specimen was found by R. E. Thaden in a road cut along Kentucky Highway 206 south of the bridge crossing the Green River north of Columbia in the Knifley quadrangle, south-central Adair County, Kentucky (approx. lat. 37° 11′ 19″ N., long. 85° 07′ 36″ W); the fossiliferous bed is approximately 4 ft below the top of the Chattanooga Shale. According to J. W. Huddle (personal communication 1970), the Chattanooga Shale is presumably of Late Devonian age in all of Adair County.

DESCRIPTION OF SPECIMEN

As a matter of general orientation it may be helpful first to refer to Plate 1 which shows the central stele and a representative sector of the tissues peripheral to it. The cylindrical core of primary xylem (X) measures 3 mm in diameter; a few radially aligned tracheids surround this in some of the thin-section preparations. There follows a narrow band of poorly preserved tissue that we interpret as phloem. Outside this there is a very narrow inner cortex (IC) in the form of a thin cylinder with regularly spaced arches that extend inward to the xylem; the greater part of the axis is made up of a broad middle cortex (MC) and a sharply defined outer cortex (OC).

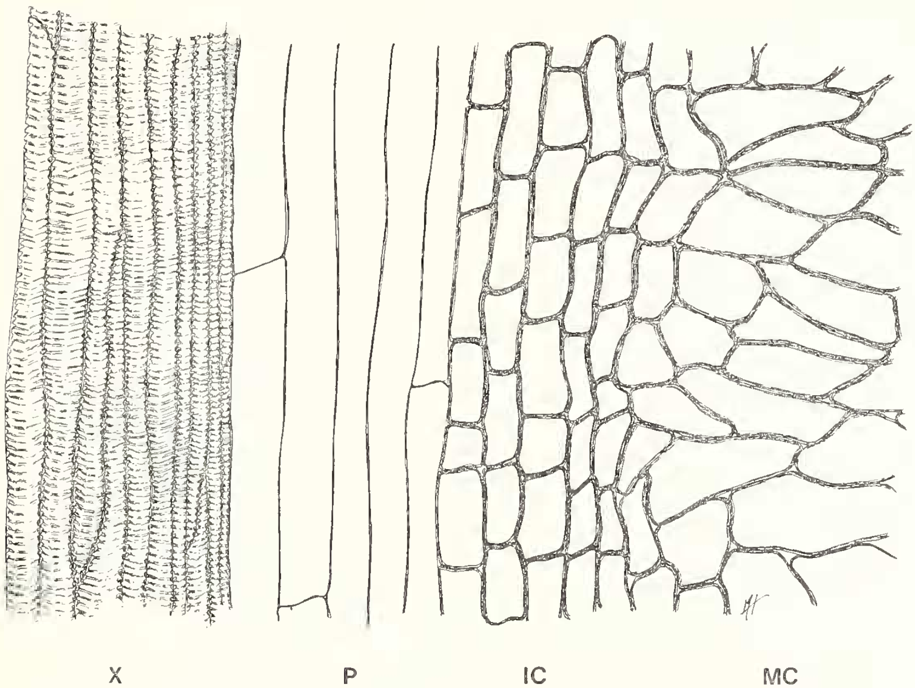
The primary wood (Pl. 2, figs. 1, 3) has the form of a nearly perfect cylinder, there being only slight fluting at the periphery. It is composed entirely of scalariform tracheids; the outermost ones are quite small, ranging from about 14×14 μm to 26×20 μm in diameter while those towards the centre are appreciably larger, attaining dimensions of 90×120 μm.

The primary wood cylinder is surrounded by a band of radially aligned secondary, tracheids, two to four cells thick. This band was apparently produced by a vascular cambium and is not only narrow but also irregular in amount (Pl. 2, figs. 2, 3); it is in fact so narrow and irregular in development and the tracheids, at many points so similar in size to those of the primary wood, that it is difficult to distinguish it in longitudinal section.

Immediately peripheral to the xylem there is a band of phloem and inner cortex; in view of the way in which they are associated it seems expedient to deal with them together. The inner cortex (Pl. 1; Pl. 2, figs. 2, 3) is a continuous band some 10–12 cells thick radially; it is separated from the outermost xylem by a distance of about 0·3 mm except that there are rather regularly spaced arches or bridges (about 0·6 mm apart tangentially) which extend into, and are in contact with, the xylem. There is thus a ring of tangentially elongate spaces between the xylem and inner cortex which we interpret as the site of the phloem (Pl. 2, fig. 2).

In transverse section the inner cortical cells appear a little less angular than the tracheids and intercellular spaces were probably present. The cells range from 24 to 50 μm in diameter with many of them very close to 35 μm. In longitudinal view (text-fig. 1) they are readily distinguished from any other tissue; they are elongate, varying from 45 to 185 μm, with transverse or oblique end walls. The leaf traces depart through the arches of inner cortex and will be considered separately.

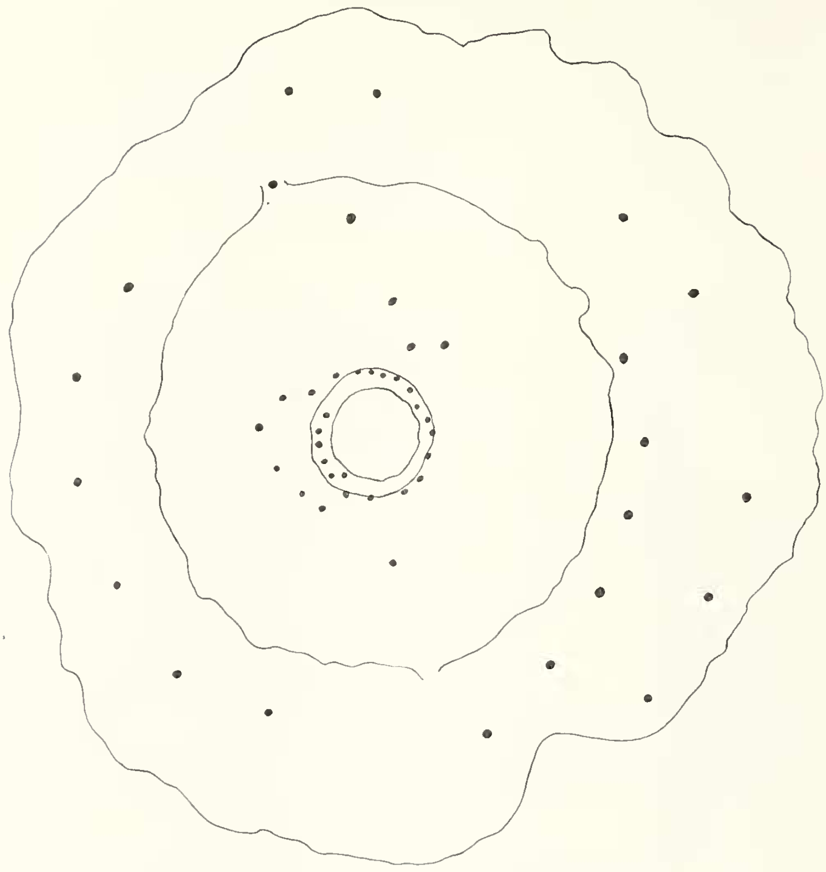
The oval-shaped (in transverse section) phloem areas between the xylem and inner cortex constitute the only poorly preserved tissue in the specimen. In most of our preparations the central part of the phloem has been lost through decay; in Plate 2, fig. 3, there are a few phloem cells immediately outside the xylem and a few just within the inner cortex. One of our longitudinal sections, however (slide 7) shows cellular continuity between the xylem and inner cortex. Between these two tissues (text-fig. 1) there are greatly elongate, thin-walled cells about 30 μm in diameter; it is presumed that they are sieve cells or the functional equivalent of sieve cells of modern vascular plants, although no pitting details have been observed. It was not possible to obtain a satisfactory photograph of this zone and text-fig. 1 is offered as a camera lucida drawing which shows the size and relationships of the tissue systems from the periphery of the xylem to the inner margin of the middle cortex.



TEXT-FIG. 1. A drawing of a portion of slide no. 7 showing: X, peripheral part of xylem; P, phloem; IC, inner cortex; MC, inner part of middle cortex.

The middle cortex (Pl. 1, MC; Pl. 3, figs. 1–3) is, to the best of our knowledge, a unique tissue but if not unique it is most unusual. It is about 5 mm in radial thickness and consists of two fairly distinct types of cells: a groundwork of large, thin-walled irregularly shaped cells that is traversed by more or less radially aligned strands of elongate cells. These strands tend to stand out most conspicuously at lower magnifications (Pl. 1). Although essentially radially aligned they may be irregular and tend to anastomose and divide (Pl. 3, fig. 1). The great variation in their size is apparent in a tangential-longitudinal section (Pl. 3, fig. 2) where they appear as clusters of small cells (about 3–30) scattered among the larger cells of the ground tissue. It is even more difficult to delimit the strands in a radial section (Pl. 3, fig. 3).

The outer cortex is also broad and distinctive. It is 5–6 mm wide (Pl. 1, OC), and consists of cells that seem best described as short fibres. In a transverse section they



TEXT-FIG. 2. Diagram of a transverse section showing leaf trace distribution; slide H1.

appear quite uniform in size and shape, ranging from 85 to 105 μm in diameter. In longitudinal view (Pl. 2, fig. 5; Pl. 4, fig. 2) they appear elongate with tapered ends and range from 0·75 to 1·2 mm long. Intercellular spaces at the corners of the cells are quite

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EXPLANATION OF PLATE 1

Fig. 1. A representative sector of the stem in transverse section. X, cylindrical core of primary xylem; IC, inner cortex; MC, middle cortex; OC, outer cortex. Slide H1; ×14.

EXPLANATION OF PLATE 2

Fig. 1. The xylem. X, primary xylem; SX, the narrow band of radially aligned tracheids, presumably secondary xylem. Slide H1; ×33.

Fig. 2. Portion of the central part of the stem from the periphery of the primary xylem to the inner part of the middle cortex. X, primary xylem; PH, areas that were occupied by phloem; IC, inner cortex; LT, leaf traces; MC, inner part of the middle cortex. Slide H1; ×46.

Fig. 3. A portion of fig. 2, enlarged. LT, leaf traces; IC, inner cortex; PH, phloem. Slide H1; ×140.

Figs. 4, 5. Transverse and radial-longitudinal sections, respectively, ×140, showing the contact between middle and outer cortices. MC, middle cortex; OC, outer cortex, 4, slide H1. 5, slide 4.

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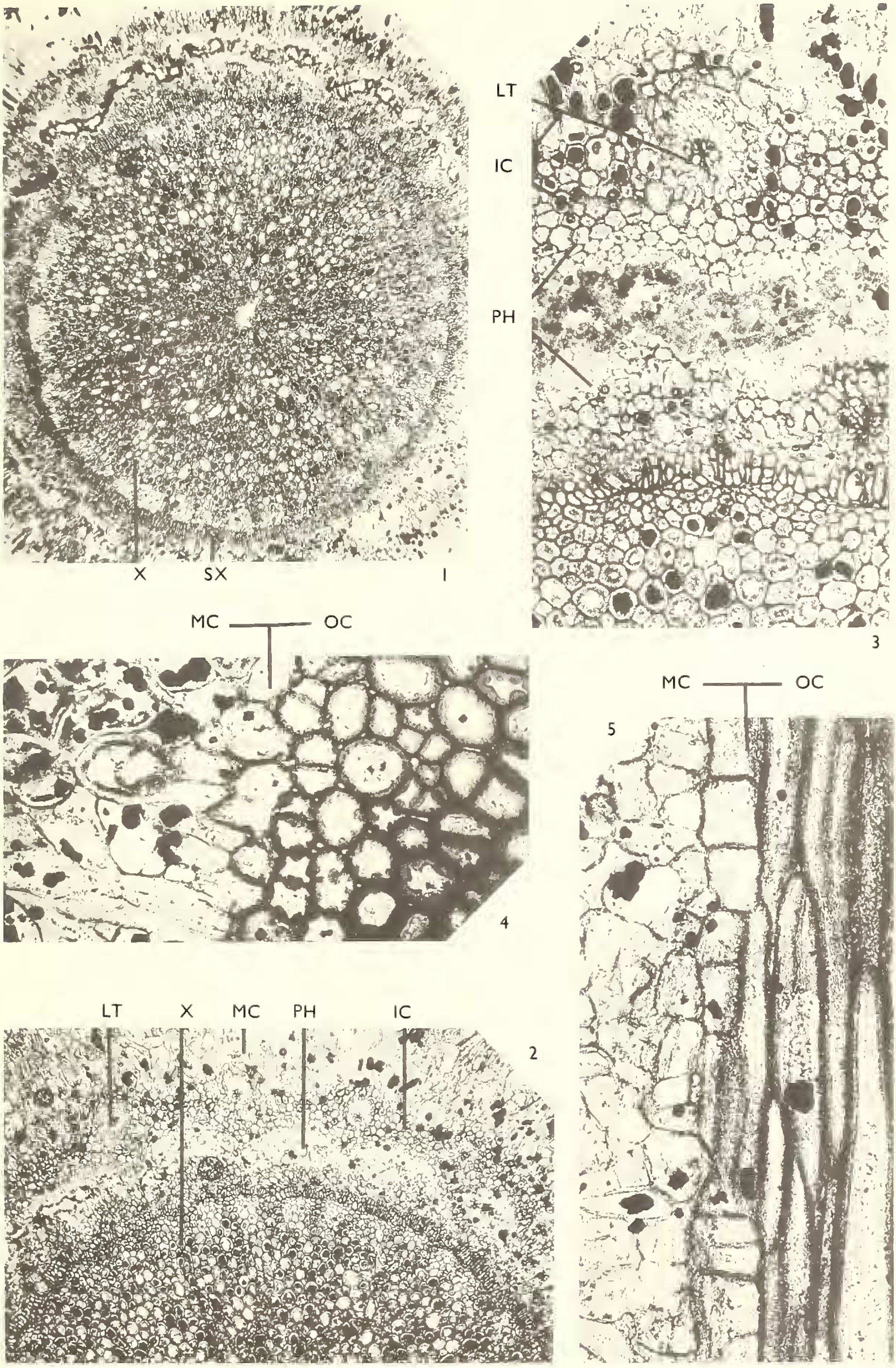

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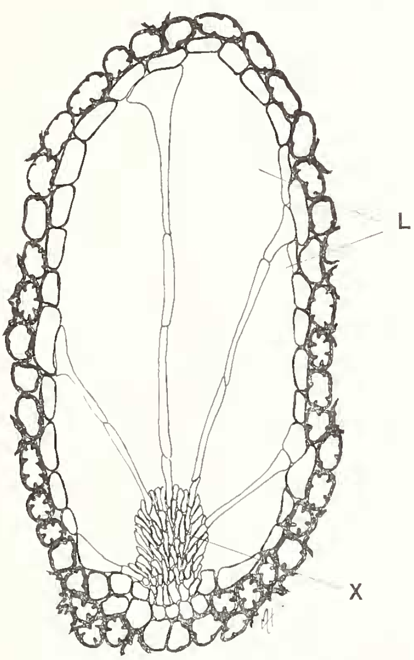
conspicuous and the walls are irregularly thickened (Pl. 2, fig. 4; Pl. 4, fig. 4). The latter feature varies considerably as may be noted in Plate 2, fig. 4; although we are inclined to regard it as a natural feature it is possible that it is due in part to alterations of the cell walls during fossilization.

In some of our sections sporadic patches of radially aligned cells may be observed at the periphery of the outer cortex (Pl. 4, fig. 3) and at the outer margin of the middle cortex (Pl. 3, fig. 4).

The leaf traces depart from the periphery of the primary xylem. Where they are particularly well preserved (Pl. 2, fig. 3) it may be observed that they consist of a small central strand of about a dozen annular tracheids surrounded by very thin-walled cells that are presumed to be phloem; this phloem sheath is usually one cell thick on the inner and lateral sides of the tracheidal strand and three to four cells thick on the outer side. The leaf traces depart from the xylem core in a helical arrangement but the angle of the spiral is so low as to present a nearly whorled arrangement. Several traces are evident in Plate 2, fig. 2 where they are passing through the outer part of the inner cortex.

The traces are particularly conspicuous in the outer cortex and parts of two 'whorls' are evident in Plate 1; see also text-fig. 2. Reference should be made to Plate 4, fig. 1 and text-fig. 3 for details of the trace in this part of the stem. The trace itself remains attached to the inner wall of the apparent gap; this is evident in the ring of traces in the inner part of the outer cortex in Plate 1. The oval-shaped gap (trabecula) has not resulted from decay but is a natural chamber (text-fig. 3) and several delicate parenchymatous strands serve to attach the trace to the wall of the chamber. These slender, multicellular filaments which traverse the trabecula are generally poorly preserved but in a few instances they are intact. It seems probable that the trabeculae facilitated the passage of oxygen from the leaves through the outer cortex, which must have been otherwise quite impermeable. Diffusion of oxygen through the middle cortex was presumably much more readily achieved by virtue of the parenchymatous cell structure and, in some lycopods, by the presence of intercellular spaces.



TEXT-FIG. 3. A leaf trace in the outer cortex, transverse section showing xylem strand and lacunae; slide A3.

The leaf traces form an acute angle with the long axis in the inner and outer cortex; thus in a transverse section of the axis the traces too are cut in a near-transverse section and are quite readily discernible. They follow a more nearly horizontal course in the middle cortex and it is difficult to distinguish them from the numerous black pyrite particles that are especially abundant in the cells of this tissue. Also, the chambered cavities, which render the location of the traces so distinct in the outer cortex, are lacking in the middle cortex.